directly record neural activities during behavior.

References

1. Yang, J.F. (2006). Spinal and brain control of human walking: implications for retraining of walking. Neuroscientist *12*, 379–389.
2. Büschges, A. (2005). Sensory control and organization of neural networks mediating coordination of multisegmental organs for locomotion. J. Neurophysiol. *93*, 1127–1135.
3. Yellman, C., Tao, H., He, B., and Hirsh, J. (1997). Conserved and sexually dimorphic behavioral response to biogenic amines in decapitated *Drosophila*. Proc. Natl. Acad. Sci. USA *94*, 4131–4136.
4. Harley, C.M., English, B.A., and Ritzmann, R.E. (2009). Characterization of obstacle negotiation behaviors in the cockroach, *Blaberus discoidalis*. J. Exp. Biol. *212*, 1463–1476.
5. Cowan, N.J., Lee, J., and Full, R.J. (2006). Task-level control of rapid wall following in the American cockroach. J. Exp. Biol. *209*, 1617–1629.
6. Strauss, R. (2002). The central complex and the genetic dissection of locomotor behaviour. Curr. Opin. Neurobiol. *12*, 633–638.
7. Homberg, U. (1987). Structure and functions of the central complex in insects. In Arthropod Brain: Its Evolution, Development, Structure and Functions, A.P. Gupta, ed. (New York: Wiley), pp. 347–367.
8. Strausfeld, N.J. (1999). A brain region in insects that supervises walking. Prog. Brain Res. *123*, 273–284.
9. Bender, J., Pollack, A., and Ritzmann, R.E. (2010). Neural activity in the central complex of the insect brain is linked to locomotor changes. Curr. Biol. *20*, 921–926.
10. Strauss, R., Hanesch, U., Kinkelin, M., Wolf, R., and Heisenberg, M. (1992). *no-bridge* of *Drosophila melanogaster*: portrait of a structural mutant of the central complex. J. Neurogenet. *8*, 125–155.
11. Cruse, H., Dürr, V., and Schmitz, J. (2007). Insect walking is based on a decentralized architecture revealing a simple and robust controller. Phil. Trans. R. Soc. A *365*, 221–250.
12. Muller, M., Homberg, U., and Kuhn, A. (1997). Neuroarchitecture of the lower division of the central body in the brain of the locust (*Schistocerca gregaria)*. Cell Tiss. Res. *288*, 159–176.
13. Ridgel, A.L., Alexander, B.E., and Ritzmann, R.E. (2006). Descending control of turning behavior in the cockroach, Blaberus discoidalis. J. Comp. Physiol. A *193*, 285–402.
14. Gruhn, M., Zehl, L., and Büschges, A. (2009). Straight walking and turning on a slippery surface. J. Exp. Biol. *212*, 194–209.
15. Neuser, K., Triphan, T., Mronz, M., Poeck, B., and Strauss, R. (2008). Analysis of a spatial orientation memory in *Drosophila*. Nature *453*, 1244–1247.
16. Palmer, L.R., Diller, E.D., and Quinn, R.D. (2009) Design aspects of a climbing hexapod. In Proc. of CLAWAR'09: 12th International Conference on Climbing and Walking Robots, Istanbul, Turkey, pp. 197–204.
17. Wessnitzer, J., and Webb, B. (2006). Multimodal sensory integration in insects—towards insect brain control architectures. Bioinsp. Biomim. *1*, 63–75.

JC Edwards School of Medicine, Marshall University, Huntington, WV 25701, USA.
E-mail: Sensillum@aol.com

DOI: 10.1016/j.cub.2010.03.049

Evolutionary Biology: Speciation on Islands

One of the strongest rules of biological diversity — the observation that more species live on large islands than on small ones — is usually attributed to the balance between colonization and extinction. But speciation on islands cannot be ignored.

Daven C. Presgraves and Richard E. Glor

Three pivotal advances in evolutionary and ecological thinking were inspired by, of all things, the numbers and kinds of birds on islands. First, subtle differences among mockingbirds of the Galapagos Islands undermined Darwin's faith that species were the immutable products of special creation [1]. Later in life, Darwin reflected in his *Autobiography* that he had been "deeply impressed… by the South American character of most of the productions of the Galapagos archipelago, and more especially by the manner in which they differ slightly on each island of the group. …It was evident that such facts as these, as well as many others, could be explained on the supposition that species gradually become modified; and the subject haunted me" [2]. Second, the absence of sister species of birds on Indo-Pacific islands helped convince the ornithologist Ernst Mayr, and through his writings most evolutionary biologists, that geographic isolation is usually required for speciation [3,4]. Finally, the striking relationship between the numbers of bird species on islands and island area inspired MacArthur and Wilson's equilibrium theory of island biogeography [5,6].

The so-called species–area relationship, argued MacArthur and Wilson [5], is determined by three factors: colonization from the mainland (*M*) and *in situ* speciation (*G*) increase the number of species, while extinction (*D*) decreases the number of species. At equilibrium these three processes balance ($M + G = D$). To make their model simpler still, MacArthur and Wilson [5] discounted the contribution of *in situ* speciation and focused exclusively on the equilibrium between colonization and extinction, noting that "for most cases it is probably safe to omit *G* from the model" (p. 380). Under their model, then, larger islands tend to have more species because they receive more colonizing migrants and experience less extinction than small ones.

Dropping within-island speciation from the original theory seemed sensible as MacArthur and Wilson's [5] main purpose was "to express criteria and implications for the equilibrium condition without extending them for the present beyond the Indo-Australian bird faunas" (p. 386). Several studies before and since largely support the decision to disregard *in situ* speciation for birds [3,4,7,8]: only the largest islands provide opportunities for geographic isolation and *in situ* speciation in taxa that are so mobile. But by 1967, MacArthur and Wilson's [6] classic book-length treatment, *The Theory of Island Biogeography*, presented a general theory of the species–area relationship that also assumed away *in situ* speciation — a decision that implicitly assumes that all species have bird-like powers of dispersal.

Doubts about dismissing *in situ* speciation are hardly new (reviewed in [9]), but the ability to distinguish colonization and *in situ* speciation was difficult prior to the availability of modern phylogenetic analyses (Figure 1). With this evolutionary insight, calls for a new and integrated theory of island biogeography have intensified [10–14]. In an impressive new meta-analysis, Kisel and Barraclough [15] test predictions originating from earlier phylogenetic studies of the species–area relationship in *Anolis* lizards of the Caribbean [13] and bulimulid snails of the Galapagos [16]. These earlier studies revealed two major findings: first, *in situ* speciation happens on

islands having a minimum threshold area; and second, above that threshold, the probability of *in situ* speciation is positively correlated with island area. To test these predictions across the broadest array of taxa possible, Kisel and Barraclough [15] rely on taxonomic assessments as a proxy for phylogenetic relatedness, an assumption that is justified by more detailed phylogenetic analyses of many taxa in their study. To lizards and snails, the authors add ferns, flowering plants, butterflies, birds, carnivores, and bats surveyed from islands ranging in area from <1 km^2 (Nihoa) to >500,000 km^2 (Madagascar).

Not only do lizards [13] and snails [16] need less space for speciation than birds, but Kisel and Barraclough show that assuming away *in situ* speciation won't do for many other taxa either. For highly mobile taxa, such as birds, bats, and butterflies, *in situ* speciation is absent except on the very largest islands; but for less mobile taxa (the majority) the species–area relationship depends more critically on a *speciation*–area relationship. Ferns provide an interesting exception: the probability of speciation in ferns is similar on small and large islands. One possible explanation is that ferns, which are well known for their propensity to achieve instantaneous reproductive isolation via polyploidy, need no geographic isolation. When it comes to *in situ* speciation, then, biology matters, and all taxa are not equal.

Neither are all islands equal. Kisel and Barraclough [15] use multivariate analyses to disentangle the relative contributions of island area, elevation, age, and insularity (distance from mainland). Decoupling island area from elevation is especially important, as higher probabilities of *in situ* speciation on large islands might reflect their greater opportunity for geographic isolation (and hence allopatric speciation) or their greater habitat diversity (and hence ecological speciation). Island elevation serves as a useful proxy for habitat diversity as other systematic measures are difficult to come by (but see [16]). Although Kisel and Barraclough [15] find that island area is the strongest predictor of the probability of *in situ* speciation, elevation and insularity are also important predictors. Age, however, is not, suggesting that islands may quickly achieve colonization-speciation-extinction equilibrium. Species diversity may therefore be more limited by ecology than the intrinsic rate at which a taxon can produce new species [17].

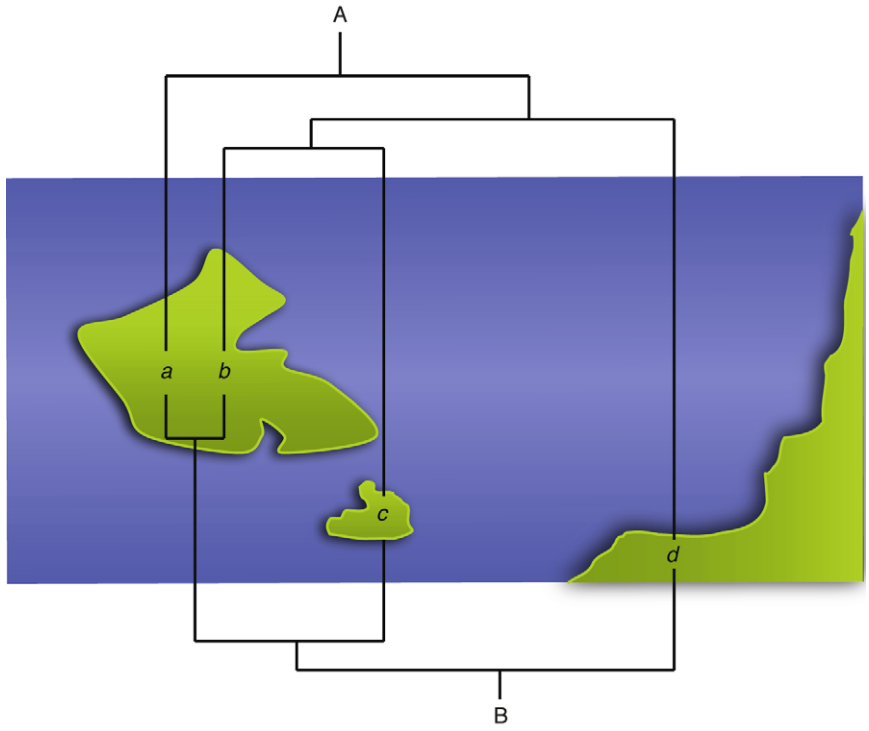

Figure 1. Phylogenetic analyses combined with geographic data can distinguish colonization from *in situ* speciation.

The top phylogenetic history (A) shows that species *a* and *b* are not sister species and are thus not necessarily the products of *in situ* speciation. Instead, species *b* and *c* are sister species, consistent with inter-island speciation. The bottom phylogenetic history (B) shows that species *a* and *b* are sister species on the same island, consistent with *in situ* speciation.

Kisel and Barraclough [15] push their analysis one step further, asking if taxon-specific spatial scales of population genetic differentiation are associated with the probability of *in situ* speciation. Speciation is a continuous process in which isolated populations gradually accrue, first, allele frequency differences, then fixed genetic differences, and ultimately functional genetic differences that cause reproductive isolation. Taxa able to accumulate population genetic differentiation on small geographic scales should also show small minimum threshold areas and higher probabilities of speciation. Consistent with this prediction, Kisel and Barraclough [15] find that, at the scale of 10–100 km distances, snail populations accumulate considerable genetic differentiation whereas bat populations do not. Thus, *in situ* speciation contributes to local species diversity only when gene flow is unable to prevent population genetic differentiation — when islands are sufficiently large, when species are sufficiently sedentary, or both.

Kisel and Barracough's [15] results powerfully reinforce the assertion that any general explanation for the species-area relationship must include speciation. Their work also shows that biological details, like the capacity to disperse and mode of speciation, are critical parameters for new theories of island biogeography (see also [9,12,18]). Other major features of the species-area relationship remain largely unexplored, including the pattern of species accumulation over time (for example, fast early on, slow later) and the relative contributions of *in situ* speciation *versus* colonization. Phylogenetic studies are limited by their inability to include extinct lineages and by the tendency for the scope and accuracy of historical inference to decay with time. Nevertheless, we are likely entering a period during which increasingly well-resolved and

comprehensively-sampled phylogenetic analyses will permit new insight on the evolution of major patterns of biological diversity.

References

1. Sulloway, F.J. (1982). Darwin's conversion: the *Beagle* voyage and its aftermath. J. Hist. Biol. *15*, 325–396.
2. Barlow, N., ed. (1958). The Autobiography of Charles Darwin (New York: W.W. Norton & Company).
3. Mayr, E. (1940). Speciation phenomena in birds. Am. Nat. *74*, 249–278.
4. Mayr, E. (1942). Systematics and the Origin of Species (New York: Columbia University Press).
5. MacArthur, R.H., and Wilson, E.O. (1963). An equlibrium theory of insular zoogeography. Evolution *17*, 373–387.
6. MacArthur, R.H., and Wilson, E.O. (1967). The Theory of Island Biogeography (Princeton, NJ: Princeton University Press).
7. Coyne, J.A., and Price, T.D. (2000). Little evidence for sympatric speciation in island birds. Evolution *54*, 2166–2171.
8. Diamond, J.M. (1977). Continental and insular speciation in Pacific land birds. Syst. Zool. *26*, 263–268.
9. Lomolino, M.V., and Brown, J.H. (2009). The reticulating phylogeny of island biogeography theory. Quart. Rev. Biol. *84*, 357–390.
10. Heaney, L.R. (2000). Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium theory of island biogeography. J. Biogeogr. *9*, 59–74.
11. Heaney, L.R. (2007). Is a new paradigm emerging for oceanic island biogeography? J. Biogeogr. *34*, 753–757.
12. Lomolino, M. (2000). A call for a new paradigm of island biogeography. Global Ecol. Biogeogr. *9*, 1–6.
13. Losos, J.B., and Schluter, D. (2000). Analysis of an evolutionary species-area relationship. Nature *408*, 847–850.
14. Whittaker, R.J., Triantis, K.A., and Ladle, R.J. (2008). A general dynamic theory of oceanic island biogeography. J. Biogeogr. *35*, 977–994.
15. Kisel, Y., and Barraclough, T.G. (2010). Speciation has a spatial scale that depends on levels of gene flow. Am. Nat. *175*, 316–334.
16. Parent, C.E., and Crespi, B.J. (2006). Sequential colonization and diversification of Galapagos endemic land snail genus *Buliminus* (Gastropoda, Stylommatophora). Evolution *60*, 2311–2328.
17. Rabosky, D.L. (2009). Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. Ecol. Lett. *12*, 735–743.
18. Losos, J.B., and Parent, C.E. (2009). The speciation-area relationship. In The Theory of Island Biogeography at 40: Impacts and Prospects, J.B. Losos and R.E. Ricklefs, eds. (Princeton, NJ: Princeton University Press).

Department of Biology, University of Rochester, Rochester, NY 14627, USA.
E-mail: dvnp@mail.rochester.edu

DOI: 10.1016/j.cub.2010.03.032

Vision: Keeping the World Still When the Eyes Move

A long-standing problem for visual science is how the world remains so apparently stable in the face of continual rapid eye movements. New experimental evidence, and computational models are helping to solve this mystery.

David C. Burr[1,2] and Maria Concetta Morrone[3,4]

In a recent issue of *Current Biology*, De Pisapia, Kaunitz and Melcher [1] report a new study investigating how the world remains stable in the face of the continual rapid movements of the eyes, called saccades. Visual stability is an old and venerable problem, which has fascinated many scientists, including Descartes, Helmholtz, Mach and Sherrington. Indeed it goes back to the 11th century Persian scholar Abū ibn al-Hasan ibn al-Haytham (Latinized "Alhazen"), who, like many to follow him, put the stability down to the visual system adapting itself to the situation: "sight has become accustomed to the motion of the objects' forms on its surface when the objects are stationary, and therefore does not judge the objects to be in motion" [2]. MacKay [3] took this idea a step further, proposing that saccades form an essential part of active vision, just as exploring a surface with hand-movements is for the haptic system. Saccades, he claimed, "are perceptual questions posed by the visual system", questions like "what is that red blob over there?" The saccade brings the high-resolution fovea to bear on the object of interest, to answer the question. As the system has asked this question, it will not be surprised by the answer, provided it is roughly consistent with expectations. MacKay's idea was innovative and clearly ahead of its time, viewing eye movements as an integral part of active perception rather than an awkward consequence of a motor action. But there remains the non-trivial issue of what neural mechanisms distinguish image motion caused by movement of the eye from that caused by object-motion, and how these permit the seamless transition from one fixation to the next.

Recent research has shown that saccadic eye-movements have many transient but profound perceptual and neurophysiological ramifications. Low-frequency, fast-moving stimuli are hard to see at the time of saccades [4], possibly reflecting suppression of neurons in the superior colliculus which respond well to these types of stimulus (see [5]). This suppression could subdue the sense of motion elicited by the eye sweeping rapidly over the scene. But far more bizarre things happen than a simple reduction of sensitivity. Stimuli briefly displayed just before a saccade are grossly mislocalized, by up to 10° for a 20° saccade. The mislocalization tends to be towards the saccadic target [6], resulting in a compression of space. More recent results show that stimuli are also mislocalized in time, delayed and compressed as they are in space [7,8].

The new study of De Pisapia *et al.* [1] shows that making saccadic eye movements can actually enhance (rather than degrade) the visibility of a brief peri-saccadic stimulus. They presented a brief visual target, followed at various intervals by a surrounding annulus 'mask', which impedes recognition of the test by 'backward masking'. The most interesting condition was when test and mask were separated by a brief (12 ms) interval, both presented to stationary eyes, at the same retinal position. When presented 20–30 ms before saccadic onset, visibility of the test improved considerably, particularly for trials where it was perceived as displaced. The results imply that the peri-saccadic displacement of the test shifts it away from the mask, effectively *demasking* it. In another condition, they used a long test-mask separation with the test and mask straddling the saccade, therefore stimulating distinctly different retinal positions: yet the masking was strong, suggesting that the representation had been transferred